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BENTHIC RECOLONIZATION PATTERNS IN THE VERMILION RIVER, OHIO

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ABSTRACT

Two recolonization studies were performed in the Vermilion River, Ohio, by planting invertebrate-free sedimentary "islands" in the substratum and then collecting them at predetermined intervals. Every macroinvertebrate taxon found living on the undisturbed sedimentary bottom appeared on the islands by the 5th week in the first study and by the 24th day in the second study.

Drift was likely an important source of organisms in the early stages of recolonization. Nevertheless, the taxonomic composition of the sedimentary islands was not entirely predicted by the total composition of the drift fauna.

Compared to the marine environment, the pattern of recolonization in the Vermilion River is not established mainly through reproductive events but rather by the relative mobility and abundance of the organisms involved. Also, the time involved in complete recolonization is much less for the Vermilion River. This rapid recolonization ability of lotic benthos helps insure survival of the various species by aiding their wide dispersal within their habitat.

INTRODUCTION

By a series of experiments in which he observed the recolonization by benthic macroinvertebrates of sedimentary "islands" planted on the sublittoral sediments of Long Island Sound, McCall (1977) conclusively demonstrated that studying recolonizing processes in aqueous environments can provide important insights into the structure and dynamics of benthic communities. Furthermore, he showed that such experiments can also provide information regarding the patterns and rates by which benthic communities recover from local disasters such as pollution events.

Like McCall's, most colonization or recolonization studies which are based in aquatic environments are generally concerned with macrobenthos (particularly invertebrates) and involve the marine realm. A summary of the scope and significance of many of these marine-based studies is currently being prepared (McCall et al., in *prepr.*). By contrast, there are noticeably fewer macrobenthos colonization or recolonization studies for freshwater environments. Those involving lentic environments are often concerned with changes in species composition, richness, and abundance that occur when a new lake is created or an existing dry lake refilled (e.g., McLachlan and McLachlan, 1971; Paterson and Fernando, 1969; McLachlan, 1975). Experiments based in lotic environments generally fall into one of the following three categories: 1) the recovery of benthos after pollution abatement (e.g., Brinkhurst, 1965; Crisp and Gledhill, 1970); 2) the colonization of introduced artificial or natural substrata as a means of benthic sampling (e.g., Mason et al., 1970; Coleman and Hynes, 1970; Glime and Cleman, 1972); and 3) the sources (i.e., by drift, upstream migration, etc.) of recolonizing organisms (Waters, 1964; Williams and Hynes, 1976). A single study involving macroinvertebrates was concerned with colonization patterns on artificial substrata in relation to the MacArthur-Wilson equilibrium model (Dickson and Cairns, 1972; see also MacArthur and Wilson, 1963). Lotic environments in general are not extensively studied in terms of macrobenthic recolonization.

The main purpose of this paper is to provide new information concerning little-known aspects of recolonizing processes involving lotic macroinvertebrates, including the sequence of appearance of different organisms during recolonization, the relative efficiency of various organism sources with respect to rates of recolonization, the time involved in a complete recolonization cycle, and the way in which the overall aspect of lotic recolonization is comparable to recolonization patterns in other environments. It is hoped that this information will not only provide a more comprehensive view of recolonization processes in aquatic systems in general, but will also provide a more complete understanding of how rapidly river beds may recover biologically from local disasters. Additionally, this paper presents the first published account of the dynamics of benthos of the Vermilion River, Ohio. The Vermilion is one of several similar, little-studied northern Ohio rivers that empty into Lake Erie. Information for this study was collected by the author during July-September 1975 from the Vermilion River, Ohio.

STUDY AREA

The Vermilion River arises in the community of Bailey Lake (Ashland Co.), Ohio, where it is the main outlet of Mud Lake (40° 57' N, 82° 21' W).

According to the Ohio Division of Water (1954), the river is 94.4 km long and drains an area of 703.4 km². The elevation at the source is 313.9 m, and the average fall is 1.5 m/km (all units here converted to the metric). The mouth of the river is in the town of Vermilion (Erie Co.), Ohio, where the river empties into Lake Erie. By interpolating figures received from the National Weather Service (personal communication) it is reasonable to estimate that the drainage basin of the Vermilion River receives about 86 cm of rainfall annually and that the average yearly temperature for the same area is approximately 10.4°C.

Excepting the last 5-6 km of the river, where it flows through suburban and urban areas and is in places noticeably polluted, all the upper reaches of the Vermilion flow through rural countryside where the chief pollutants are fine clastic sediments and fertilizers derived from agricultural operations. Inferring from the presence in the river of a variety of pollution intolerant organisms (e.g., diverse Plecoptera, Ephemeroptera, Trichoptera; Gaufin and Tarzwell, 1952, 1956; Beck, 1954), most of the upper reaches of the river are fairly clean.

The Vermilion's bed is a complex mosaic of sediments. Nevertheless, in the upper reaches of the river, the bottom is usually composed of one of two broad sedimentary suites. Where currents are more rapid, the bottom is largely composed of gravels consisting of shale, siltstone, or sandstone clasts that overlie coarse to fine sands and muds. Where currents are slower, the predominating substratum often consists of sandy muds. Species richness is usually greater on the gravelly substrata.

A small area of the river ($\sim 5 \times 15$ m) located ~ 16.5 km (river distance) from the mouth and ~ 0.6 km south of the end of Banks Road was selected for its remoteness from human disturbance and homogenous sedimentary bottom. This section has the gravelly bottom characteristic of large sections of the river and moreover, is about as rich in benthic macroinvertebrate species for any particular time of year as any other sampled area of the river (excluding riffles). During July-September 1975 the observed bottom water temperature in this area ranged from 23 to 27°C, water depth varied from 30 to 70 cm, and current velocity ranged from 4 to 18 cm/sec. Two successive recolonization experiments were subsequently performed at this site (Fig. 1.).

MATERIALS AND METHODS

The river was sampled in three ways. *Grab samples* were taken by inserting into the river bottom a plastic container open on one end. The container was placed open-end-downward and pushed vertically into the sediment until it was full. Then the surrounding sediment was dug away from the sides and bottom of the container, a cap was placed over the open end, and the

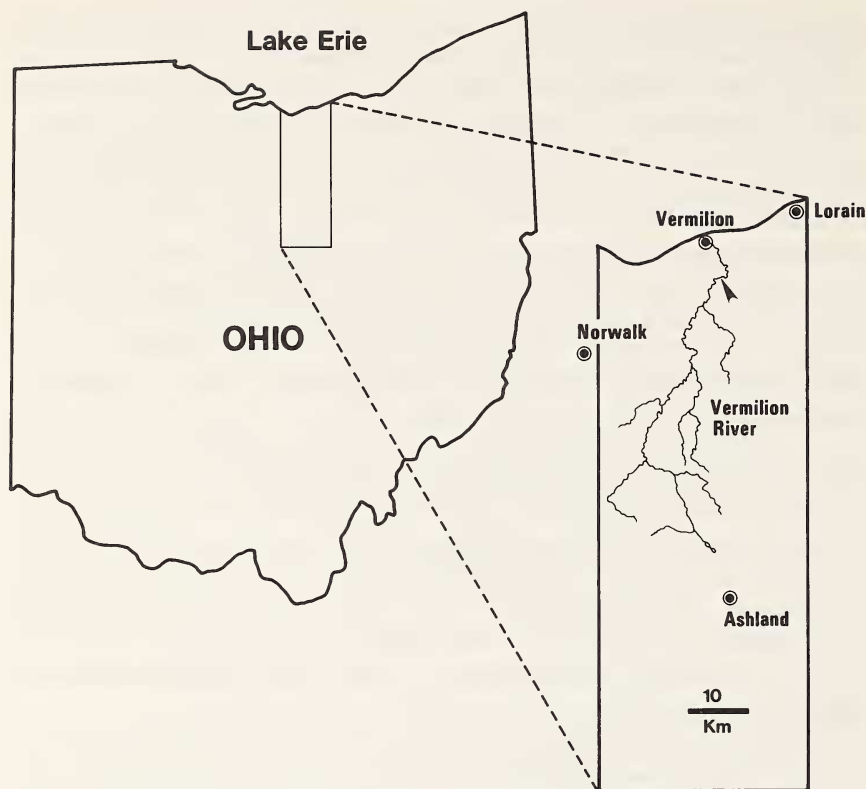


Fig. 1. Location of the Vermilion River, Ohio. Arrow indicates the study area.

container was removed from the sediment. The open end of the container measured 10 cm \times 10 cm, and its height was 14 cm. Thus each "grab" sampled about 100 cm² of bottom to a depth of 14 cm (slight flexing of the sides and bottom of the container during sampling make these figures close approximations).

Williams and Hynes (1974) show that numerous macroinvertebrates occur to depths of about 30 cm within the substrata of certain streams, with maximum organism densities occurring at 10 cm. Additionally they report a few species living at depths of up to 80 cm. Deep excavations into the substratum of the Vermilion River showed that in June-September 1975 most macroinvertebrates occurring in the study area were living in the upper 5-10 cm of the substratum. While oligochaetes were occasionally found below this level to depths of 20 cm or more, aquarium studies showed that they usually penetrated to this depth as an avoidance response to physical disturbance, and were not characteristically

living there. Since the grab samples penetrated to a depth of 14 cm, they were likely an adequate means of determining for the area they covered the abundance and taxonomic composition of most macroinvertebrate taxa excluding oligochaetes.

Recolonization samples were obtained by filling containers of the dimensions mentioned above with river sediments from the experiment site. These sediments had previously been dried, treated with boiling water, and dried again to remove all macroinvertebrates and their eggs and resting stages. The containers were capped and placed in the river in an area of substratum upstream from any previous sampling disturbance. The containers were sunk in the bottom until the lip was nearly flush with the river bed. By extending slightly above the substratum, the containers represented a small positive area on the bottom even when covered by subsequently deposited sediments. This facilitated locating the samples. The lids were then removed and the individual containers collected at predetermined intervals. Covers were placed on the containers just prior to sampling.

Removing, treating, and replanting the substratum obviously altered such properties as porosity, organic content, and probably grain size. Nevertheless, the gross physical aspects of the substratum remained the same as that of the river bed, save that it lacked macrofauna.

Rapid sedimentary accumulation (within 1-2 days) up to and over the edges of the containers meant that they were susceptible to recolonization from the four main recolonizing avenues employed by river organisms (upstream migration within the water, drift, within substratum migration, and oviposition [Williams and Hynes, 1976]).

Drift samples were obtained by attaching a net (7 threads/cm) with an opening of 32 cm to an iron support and placing it for 24 hours in the river with the open end facing upstream. The net was elevated approximately 4 cm off the bottom to exclude organisms crawling along the substratum.

Fouling of the drift net by sediments, leaves, and wood frequently occurred during the sampling interval and caused resistance to water flow through the net. This impedence to flow sometimes caused eddying near the mouth of the net, which may have lowered sampling efficiency. Thus the drift samples likely provide only a very rough estimate of the relative abundance of drifting organisms and may have excluded rare species. Although the net material consisted of 7 threads/cm, the material was fastened to the net in a double layer, and organisms less than $\frac{1}{2}$ mm in length were occasionally retained.

Approximately forty grab samples were taken in late June 1975 near the experimental sites to determine the taxonomic composition of the bottom in this section of the river. Analysis of these samples showed that over 90% of the

species sampled occurred in any given set of four samples. Also, the relative abundance of organisms in these four samples correspond to the relative abundance in all samples. So for the purposes of the experiment, the contents of four grab samples were considered representative of the fauna for this small area of river (see also Cain, 1938). Similarly, the contents of four simultaneously collected recolonization samples were considered representative of how this area would appear at a given instant of time after defaunation.

All benthic macroinvertebrates (\equiv size ≥ 1 mm) were picked by hand from all samples within 12 hours of collection. The organisms were preserved in 70% ethanol.

Two consecutive recolonization experiments were run in the following manner: For the first experiment, 20 recolonization sample "islands" were planted in the river bed on 2 July 1975. The original plan was to collect 4 boxes at a time, once a week, for 5 consecutive weeks. However, problems in locating the islands on the 3rd week of the experiment extended the experiment an extra week. The final set of 4 recolonization samples was collected on 13 August. The 4 recolonization samples were always selected at random. One drift sample was also taken simultaneously with each set of 4 recolonization samples. Experimentation with multiple drift samples revealed no noticeable differences in taxonomic composition or relative abundance of organisms among different samples. Two sets of 4 grab samples of the surrounding natural bottom were also taken during the course of the 5 week experiment.

A second experiment was initiated on 13 August when 32 defaunated sediment samples were planted in the river upstream and laterally displaced from the previous experiment site. Four recolonization samples were taken simultaneously every 3rd day. One drift sample was also taken at each sampling interval. Two sets of 4 grab samples were also taken during this time. The final set of 4 recolonization samples was collected on 6 September 1975.

RESULTS

The recolonization samples from both experiments (Tables 1, 2) show that the earliest colonizers were mostly immature Insecta. In the first experiment, all insect taxa found in the grab samples were present in the recolonization samples by the end of the first week (Tables 1, 3). In the second experiment, 4 of the 5 insect taxa found in the grab samples were also found in the recolonization samples taken 3 days after the beginning of the experiment (Tables 2, 4). Besides the immature insects, the gastropod *Oxytrema* was the only other taxon to colonize the samples during the first week. All these early colonizers were represented during the course of the experiments in the drift samples (see also Tables 5, 6).

TABLE 1
Description of Recolonization Samples for Experiment I

<i>Taxa</i>	<i>Sampling Week</i>					
	1	2	4**	5	6	
Arthropoda						
Insecta						
Diptera						
Chironomidae	18*	6*	17*	8*		14*
Coleoptera	2	0*	6	3*		0
<i>Stenelmis</i>						
Plecoptera	2	4*	8*	2*		1
<i>Acroneuria</i>						
Megaloptera	1*	1	4	0		1
<i>Sialis</i>						
Ephemeroptera	2*	8	8	2		8
<i>Hexagenia</i>						
Annelida	0	0	12	3		1
Oligochaeta						
Mollusca						
Gastropoda	1	0*	2	0		0
<i>Oxytrema</i>						
Bivalvia	0	0	0	1		2
<i>Sphaerium</i>						

key: * = Present in drift samples taken simultaneously.

** = No samples collected during week 3 of experiment.

All Insecta represented as aquatic immatures.

Organism numbers = #individuals/400 cm²

TABLE 2

Description of Recolonization Samples for Experiment II

Taxa	Sampling Period							
	(Samples taken every third day beginning Aug. 16—ending Sept. 6, 1975)							
	1	2	3	4	5	6	7	8
Arthropoda								
Insecta								
Diptera								
Chironomidae								
Coleoptera	21*	35*	51*	28	9	14	9	21
Stenelmis	1	0	0	0	0*	0	0	3
Ephemeroptera	0	0	0	1*	0*	2*	1	0
Ephemera	1*	3	1	0*	0	0*	0*	0
Heptageniidae	3*	8*	4	8*	20*	20	1*	6*
Caenidae								
Annelida								
Oligochaeta								2
Mollusca								
Gastropoda								
Oxytrema	0	1*	4*	0*	3	4*	1	1
Ferrissia								2
Bivalvia								
Sphaerium							1	1
Lasmigona								2

Key: * denotes taxa also found in corresponding drift sample.
 Organism numbers = #individuals/400 cm²

TABLE 3
Description of Grab Samples for Experiment I

Taxa	Sampling Week	
	1	2
Arthropoda		
Insecta		
Diptera		
Chironomidae	18	19
Coleoptera		
<i>Stenelmis</i>	5	3
Plecoptera		
<i>Acroneuria</i>	8	2
Megaloptera		
<i>Sialis</i>	0	2
Ephemeroptera		
<i>Ephemera</i>	8	9
Annelida		
Oligochaeta	3	4
Mollusca		
Gastropoda		
<i>Oxytrema</i>	1	1
<i>Ferrissia</i>	0	1
Bivalvia		
<i>Sphaerium</i>	1	1

All Insecta represented as aquatic immatures.

Organism numbers = # individuals/400cm²

The last organisms to appear in the recolonization samples were oligochaetes, bivalves, and the gastropod *Ferrissia*. In the first experiment, oligochaetes colonized the samples during the interval between the 2nd and 4th week, and bivalves appeared by the 5th week. In the second experiment, the oligochaetes and *Ferrissia* appeared between the sampling times of the 21st and 24th days. None of these organisms ever occurred in the drift samples. Although all taxa from the grab samples eventually appeared in the recolonization samples, these 2 kinds of samples were never identical taxonomically for any sampling period. Nevertheless, recolonization samples always grew biologically to resemble most closely the grab samples instead of the drift samples, and organisms that occurred abundantly in drift samples were sometimes uncommon or absent entirely from the recolonization samples (Compare Tables 1, 2, to Tables 5, 6).

The pattern of colonization with respect to the overall abundance of organisms was marked by large fluctuations (Figs. 2, 3). Both for the abundance pattern as a whole and with respect to any particular taxon, there were no

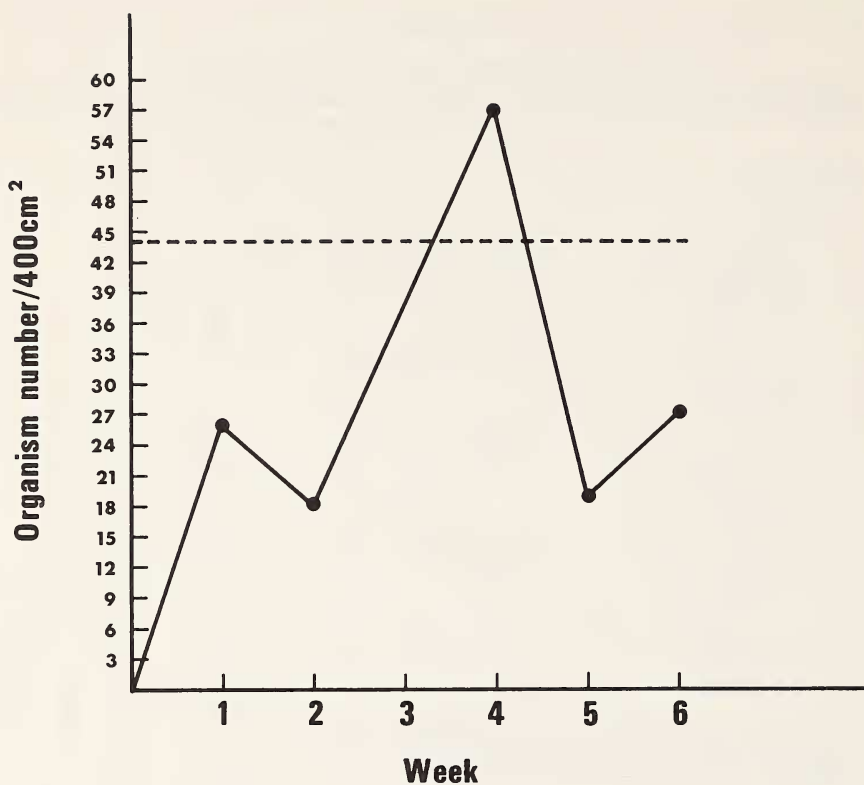


Fig. 2. Organism abundance fluctuations for the first experiment. The dashed line represents the summation of the average number of individuals per taxon collected from the grab samples.

long, uniform trends. Also, peak abundances were often reached, for each taxon and collectively, prior to the last sampling interval.

Although not all sampled organisms were measured, a qualitative assessment of their size patterns showed that this often varied widely for particular taxa within each sample and among samples taken at different times. Hence there was no discernable pattern of organism size (or age) with respect to the sequence of recolonization.

DISCUSSION

One of the main distinctions between the early and late recolonizers is that the early recolonizers are drift-prone and the later recolonizers are not. Thus drift is likely an important mechanism in the early recolonization process in the

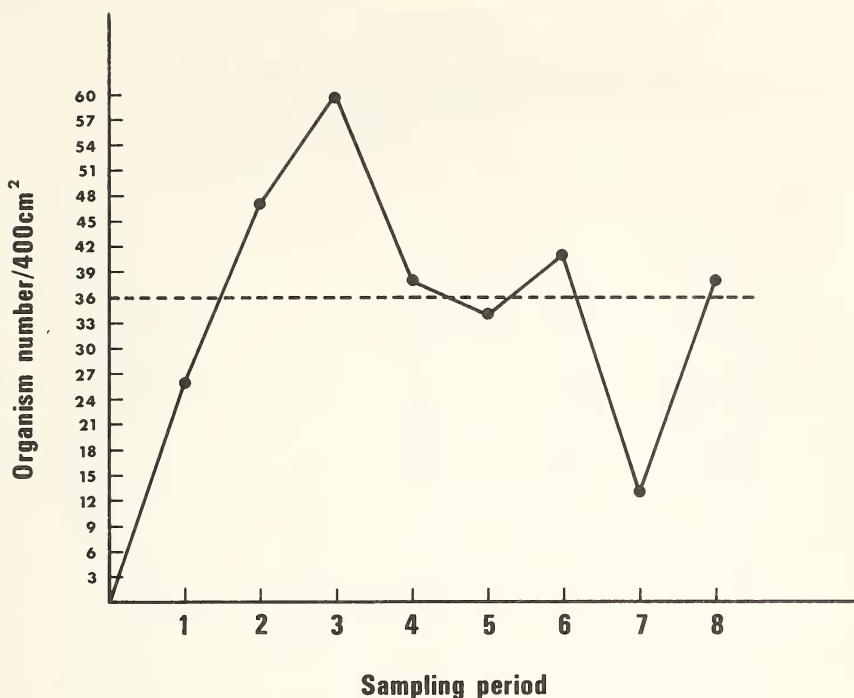


Fig. 3. Organism abundance fluctuations for the second experiment. The dashed line represents the summation of the average number of individuals per taxon collected from the grab samples.

Vermilion River. This inference is supported by Waters (1964), who shows drift to be responsible for rapid recolonization by *Baetis vagans* (mayfly) and *Gammarus limnaeus* (amphipod) in Valley Creek, Minnesota.

Nevertheless, as noted previously, the recolonization samples always more closely resembled the taxonomic composition of the grab, rather than the drift samples. This indicates that while drift is important in the early recolonizing process in this river, drift-aided recolonization is not a haphazard process dictated by the total composition of the drift fauna. Moreover, it suggests that particular organisms have an ability to select particular sites at which they may terminate drifting.

Of the other possible sources of recolonizing organisms, oviposition was likely not a major source for the Vermilion River during this time of year. Inspection of the recolonization samples showed that while the colonizing organisms varied widely intraspecifically in size, they were generally larger than they would have been had they hatched from eggs at any time during the experiment.

TABLE 4
Description of Grab Samples for Experiment II

Taxa	Sampling period	
Arthropoda	1	4
Insecta		
Diptera		
Chironomidae	25	17
Coleoptera		
<i>Stenelmis</i>	4	3
Megaloptera		
<i>Sialis</i>	1	0
Ephemeroptera		
<i>Ephemera</i>	1	0
Heptageniidae	1	1
Caenidae	5	2
Annelida		
<i>Oligochaeta</i>	4	2
Mollusca		
Gastropoda		
<i>Ferrissia</i>	1	1
<i>Oxytrema</i>	1	3
Bivalvia		
<i>Sphaerium</i>	1	1
<i>Lasmigona</i>	0	1

All Insecta represented as aquatic immatures.

Organism numbers = # individuals/400cm²

By process of elimination, the absence of oligochaetes, bivalves, and the gastropod *Ferrissia* from the drift samples indicates these organisms colonized the experimental islands by migration within the substratum or by upstream migration within the water.

Some of the early recolonizers are also more abundant on the undisturbed river bottom than are the later recolonizers (Tables 3, 4). This suggests that the higher the relative abundance of a particular taxon, the greater the chance of its being a successful early recolonizer. Thus it is entirely conceivable that highly mobile but nondrifting organisms (e.g., *Sphaerium*, *Oligochaeta*) may have appeared on the islands earlier had these taxa been more abundant.

In the sense of having 1) all taxa in the grab samples represented at some time on the islands, and 2) total organism number in the grab samples at least equaled on the islands, recolonization was complete for both experiments by the 5th week and 24th day, respectively. Although exact equivalence in taxonomic richness and organism number was not achieved between the grab

TABLE 5
Description of Drift Samples for Experiment I

Taxa	Sampling week				
	(Samples taken at weekly intervals July 9–Aug. 13, 1975)				
	1	2	4*	5	6
Arthropoda					
Insecta					
Diptera					
Chironomidae	A	A	A	A	A
Coleoptera					
<i>Psephenus</i>	C				
<i>Stenelmis (a)</i>	A		R	C	C
<i>Stenelmis</i>		C		R	
Plecoptera					
<i>Acroneuria</i>		C	R	C	
Megaloptera					
<i>Sialis</i>	R				
Ephemeroptera					
<i>Ephemer</i>	A				
<i>Callibaetis</i>	A	C	C	R	C
Heptageniidae	C				
Caenidae	C		C	R	
Trichoptera					
<i>Hydropsyche</i>	C	C			
<i>Chimarra</i>	R				
Odonata					
<i>Clithemis</i>					R
Heteroptera	C				
Corixidae					
Mollusca					
Gastropoda					
<i>Oxytrema</i>		R			
<i>Physa</i>	R				

Key: *No samples collected during week 3 of experiment

A = Abundant > 10 individuals

C = Common = 2–9 individuals

R = 1 individual

All Insecta represented are immatures unless denoted by “(a)” signifying adult.

samples and islands by the end of the experiment, the discrepancy could possibly be attributed to one or both of the following causes: 1) differences between the microenvironments of the islands and area where the grab samples were taken, and 2) unequal biotic modification of the different areas by the numerous observed storm events. These possible causes, plus the additional

TABLE 6
Description of Drift Samples for Experiment II

Taxa	Sampling period							
	(Samples taken every third day beginning Aug. 16—ending Sept. 6, 1975)							
	1	2	3	4	5	6	7	8
Arthropoda								
Insecta								
Diptera								
Chironomidae	A	A	A	A	A	A	A	A
Coleoptera								
<i>Stenelmis</i> (a)	R	R	R	C				
<i>Stenelmis</i>					R			
Plecoptera								
<i>Acroneuria</i>	R					R		
Ephemeroptera								
<i>Ephemer</i>				R	R	R		
<i>Callibaetis</i>	A			A		R	R	
Heptageniidae	A		R	A	C		R	
Caenidae	C	C		C	C		C	R
Trichoptera								
<i>Hydropsyche</i>				R				
Odonata								
<i>Clithemis</i>								R
Heteroptera								
Corixidae				C				
Mollusca								
Gastropoda								
<i>Oxytrema</i>	C	C	C			R		

Key: A = Abundant > 10 individuals
C = Common = 2–9 individuals
R = Rare = 1 individual

All Insecta represented are immatures unless denoted by “(a)” signifying adult.

factors of emergence of adult insects and possible population density regulation through drift (Waters, 1966; Dimond, 1967), might also explain the pronounced fluctuations in organism number during both experiments.

The time scale involved in the recolonization of this area of the Vermilion River is roughly similar to the findings of other workers for different streams. For example, Waters (1964) finds 1–2 days sometimes a sufficient recolonizing time for numerically dominant invertebrates in a Minnesota stream. Mason et al. (1967) suggest “about six weeks” is an adequate time for recolonization by

rock-adhering or rock-clinging invertebrates in large streams. Williams and Hynes (1976) drawing upon previously published sources, believe 28 days to be a reasonable average time for their field area in Ontario.

For the Vermilion River, this all suggests that the benthic macroinvertebrate population may rapidly recover from a local disaster if there are 1) no permanent, major, physical and chemical alterations in the environment, and 2) if there are organisms available nearby in the river to repopulate the affected area. For rivers in general, the overall kind, extent, and duration of the disaster can greatly increase this recovery time (Cairns et al. 1971).

Colonization studies that are precisely comparable to the present one are lacking for lentic environments. This is because most lentic colonization studies performed to date involve a situation in which the environment is extensively physically modified by abiotic factors prior to the completion of colonization (e.g., as in the filling of an impoundment or a dry lake; see Paterson and Fernando, 1969; McLachlan, 1975). These physical changes, such as modification of water depth and a change from a lotic to lentic system, are time consuming and may help retard the completion of colonization by a year or more.

For the marine realm, the experiments performed by McCall (1977) are not only comparable to the present study, but also provide notably contrasting results. McCall showed for Long Island Sound that most early colonizers settle from the water column onto defaunated bottom as larvae or very young juveniles. Mobility subsequent to settling is restricted. An easily recognizable succession occurs wherein opportunistic, or "r"-strategist, species initially colonize the area, only to be replaced later by more diverse assemblages of "K"-strategist species. The time for complete recolonization is approximately one year.

In the Vermilion River, recolonization takes place by either immature stages of varying age or by adults. Thus the colonization process is more of a function of relative mobility (drift, bottom migration) and relative abundance on the natural bottom and is not mainly a reproductive event. Also, no obvious pattern of succession could be identified for the Vermilion River, and the time involved in complete recolonization was much less than that for Long Island Sound.

This rapid recolonizing ability of lotic benthos is highly adaptive to the extremely rigorous physical nature of their habitat. Removal of organisms from areas of river bottom is likely a continual but spatially patchy phenomenon caused by such factors as floods, ice scour, and sediment transport. The ability of organisms to quickly recolonize areas following natural defaunation helps insure maximal dispersal within their habitat. This ability would help promote

the maintenance of high population levels within the habitat by reducing the potential for intraspecific competition. Also, wide dispersal would mean that as local populations are wiped out by changing environmental conditions, undisturbed populations of organisms are present elsewhere in the river to help insure the species' survival.

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